

Prenatal investment in the subantarctic fur seal, *Arctocephalus tropicalis*

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Abstract: We investigated prenatal investment in a large sexually dimorphic mammal, the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island in the Indian Ocean. Pups' sex ratio and body mass, body length, and body condition at birth were studied in relation to timing of birth and maternal characteristics (body length and body condition) during three consecutive breeding seasons. Pups' sex ratio did not differ from unity throughout the pupping period. The sex of the pup was related to neither maternal body length (i.e., maternal age) nor maternal body condition when mating occurred or at parturition (1 year later), which suggests that the sex ratio was not biased toward one sex during gestation. Newborn male pups were heavier and longer than female pups in all years. Longer mothers tended to arrive later in the season regardless of their body condition, and gave birth to heavier pups whatever the sex of the pup. Mothers in good condition gave birth to heavier male pups than mothers in poor condition, but no significant differences were found for female pups, suggesting that the costs of carrying male foetuses is higher than that of carrying female foetuses. Differences in allocation of maternal resources between male and female pups may be due to sex-related differences in body composition, since male pups were heavier than female pups for a given body length at birth. Thus, male and female foetuses may use maternal resources differently, with males growing in length whereas females appear to grow in body mass. The mothers we monitored over 2 consecutive years gave birth to pups that were similar in quality (in terms of birth mass) over years regardless of the sex of the previous pup and the mother's body length, suggesting that individual reproductive value is independent of maternal age. Furthermore, maternal body condition was not affected by the sex of the foetus, suggesting that there is no differential reproductive cost in carrying a male or a female foetus. Interannual differences in pup body size at birth suggest that environmental conditions such as prey availability during the last stages of gestation, and consequent maternal body condition, are important components of maternal investment in fur seals.

Résumé : Nous avons étudié l'investissement prénatal chez un grand mammifère à dimorphisme sexuel, l'Otarie à fourrure des îles Kerguelen, *Arctocephalus tropicalis*, se reproduisant sur l'île Amsterdam, dans l'océan Indien. Le rapport mâles : femelles de même que la masse, le longueur et la condition physique des nouveau-nés ont été étudiés en relation avec la date de naissance et avec les caractéristiques de la mère (taille et condition physique) durant trois saisons consécutives de reproduction. Le rapport mâles : femelles à la naissance ne diffère pas de l'unité durant la période de mise bas. Le sexe des petits n'est relié ni à la longueur de la mère (c.à.d. l'âge de la mère), ni à sa condition physique au moment de l'accouplement ou de la mise bas, ce qui indique que le rapport mâles : femelles n'avantage pas un sexe plus que l'autre pendant la gestation. Les nouveau-nés mâles sont plus lourds et plus longs que les nouveau-nés femelles chaque année. Les mères de grande taille ont tendance à arriver plus tard au cours de la saison, quelle que soit leur condition physique, et elles donnent naissance à des jeunes, mâles ou femelles, plus lourds. Les mères en bonne condition physique donnent naissance à des mâles plus lourds que les mères en mauvaise condition, mais cela n'est pas vrai pour les nouveau-nés femelles, ce qui semble indiquer que la gestation de rejetons mâles est plus coûteuse que celle de rejetons femelles. L'allocation des ressources maternelles diffère chez les nouveau-nés mâles et femelles, peut-être à cause de différences dans la composition corporelle, puisque les nouveau-nés mâles sont plus lourds que les nouveau-nés femelles de même longueur. Les fœtus mâles et femelles semblent utiliser les ressources maternelles différemment puisque les mâles croissent en longueur et les femelles en taille. Les mères suivies pendant 2 années consécutives ont donné naissance à des jeunes de qualité similaire (masse à la naissance) indépendamment du sexe du rejeton précédent et de la longueur de la mère, ce qui indique que la valeur reproductrice individuelle ne dépend pas de l'âge de la mère. De plus, la condition physique de la mère n'est pas affectée par le sexe du fœtus, ce qui permet de croire que les

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coûts liés à la reproduction sont les mêmes qu'il s'agisse de fœtus mâles ou de fœtus femelles. Des différences inter-annuelles de la taille à la naissance semblent indiquer que les conditions environnementales, telle que la disponibilité des proies, au cours des derniers mois de la gestation et la condition physique de la mère qui en découle sont des éléments importants de l'investissement maternel chez les otaries à fourrure.

Introduction

In most mammals with sexual dimorphism in body size, male breeding success depends on adult body size and consequent fighting ability (Trivers and Willard 1973; Clutton-Brock et al. 1982; Carranza 1996). In polygynous species, variance in reproductive success is usually greater among males than females (Trivers 1972; Alexander et al. 1979; Clutton-Brock 1988). In such mating systems, the reproductive success of sons should be more strongly influenced by adult body size, which is in turn dependent on early growth during the rearing period, than the reproductive success of daughters. Thus, mothers in good condition are expected to allocate more resources to sons than to daughters (Trivers and Willard 1973; Charnov 1982). Two mechanisms have been suggested for differential allocation of resources to sons and daughters at the population level: (1) Fisher (1930) hypothesised that, on average, parents divide their reproductive effort equally between the sexes so that the extra costs of rearing one sex will lead to the sex ratio being biased against the more expensive sex, and (2) when the sex ratio is mostly fixed at unity, parental reproductive effort will vary between the sexes of the offspring (Maynard Smith 1980). At the individual level, this adaptive sex bias in maternal investment will occur if the difference in offspring quality at the end of maternal investment persists to adulthood, when it will have a greater effect on male reproductive success than on female reproductive success (Trivers and Willard 1973).

Many pinnipeds show marked sexual dimorphism in body size, adult males being larger than adult females (King 1983). Males make no contribution to the rearing of the offspring. The mating system is highly polygynous and observations suggest that reproductive success varies more widely among males than among females (McCann 1980; Anderson and Fedak 1985; Le Boeuf and Reiter 1988), so Frank (1990) suggested that pinnipeds may offer a good opportunity to test parental-investment theory. However, Trillmich (1996) pointed out that available data are not sufficient to draw a general model of parental investment in this group. Furthermore, most of the studies on pinnipeds investigated maternal input (or care, e.g., resource transfer) rather than maternal investment, as the reproductive cost to the mother (reduced future reproduction) was not assessed. Body size at birth has been shown to be determinant for pup growth (Georges and Guinet 2000a, 2000b) and survival during the pup's dependence (Calambokidis and Gentry 1985; Boltnev et al. 1998), but to date there are no data on the effect of body size at birth on adult reproductive success in fur seals. Thus, investigations of prenatal investment may increase our knowledge concerning the way in which the mother's characteristics act on pup size at birth, and possibly on the consequent survival of their pups, as a step toward studying the longer term consequences of maternal care.

Equal sex ratios of pups at birth have been reported in otariids (Trillmich 1986; Ono et al. 1987; Trites 1991; Goldsworthy and Saughnessy 1994). In several studies it was as-

sumed that the energetic cost of gestation was likely to be higher for male offspring than for females because males are heavier than females at birth (Trillmich 1986; Boyd and McCann 1989; Lunn and Boyd 1993a; Ono and Boness 1996). However, body composition should also be taken into account because, despite differences in body mass, the total amounts of energy may be similar (Stamps 1990). For example, female Antarctic fur seal (*Arctocephalus gazella*) pups are lighter but fatter than male pups, resulting in a lack of difference in total body gross energy between the sexes (Arnould et al. 1996a). In their review, Lunn and Arnould (1997) proposed that maternal investment does not differ between the sexes in Antarctic fur seals. In this species, maternal age, size, and experience appear to influence the timing of parturition, with smaller and younger females giving birth to lighter pups later in the pupping season (Boyd and McCann 1989; Duck 1990; Lunn and Boyd 1993a). In Antarctic fur seals, Costa et al. (1988) found a better correlation between maternal mass and pup mass at birth for female pups than for male pups. However, Boyd and McCann (1989) found no correlation between maternal mass and female pup mass at birth, although mothers in good condition gave birth to heavier male pups than mothers in poor condition. Differences in environmental conditions and maternal state between the two studies are thought to be responsible for these different relationships (Trillmich 1996).

In this paper we investigate the relationships between maternal and pup characteristics at birth in the subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island in the Indian Ocean. We monitored the sex ratio, body mass, body length, and body condition of pups at birth in relation to maternal body length and condition and timing of birth during three consecutive breeding seasons. In this sexually dimorphic and polygynous species, mothers are expected to allocate more resources to male than to female pups, either by biasing the sex ratio at birth or by transferring more resources to male than to female pups. If so, mothers that produced a son would be expected to produce a daughter the following year. Older (and thus more experienced) mothers and those in good condition would be expected to be more able to care for their offspring than younger mothers and those in poor condition.

Methods

Study site and animals

This study was carried out during the austral summers of 1994–1995, 1995–1996, and 1996–1997 (hereinafter referred to as 1995, 1996, and 1997) at La Mare aux Elephants breeding colony on Amsterdam Island (37°55'S, 77°30'E) (Guinet et al. 1994). From late November to early January, a total of 981 births (232, 438, and 311 births in 1995, 1996, and 1997, respectively) were identified during daytime during continuous watch patrols within the study beach. In some cases, births were identified but pups were not measured because of the aggressive behaviour of harem bulls. Although the same colony was studied in all 3 years, the areas monitored varied, so a comparison of numbers of births among years

Table 1. Maternal body condition and birth date and sex ratio, body mass, body length, and body condition at birth for male and female subantarctic fur seal (*Arctocephalus tropicalis*) pups on Amsterdam Island during the 1995, 1996, and 1997 reproductive seasons.

	1995			1996			1997					
Maternal condition ^a	No data			113/148			73/133					
Pup sex ratio ^b	114/118			222/216			138/173					
Birth date												
Male pups	13 Dec. ± 7.4 days (114)			14 Dec. ± 8.3 days (222)			13 Dec. ± 8.0 days (138)					
Female pups	14 Dec. ± 7.6 days (118)			14 Dec. ± 8.9 days (216)			14 Dec. ± 8.0 days (173)					
Body mass (kg)												
Male pups	4.9 ± 0.5 (114)			5.1 ± 0.6 (220)			4.9 ± 0.6 (131)					
Female pups	4.3 ± 0.6 (118)			4.5 ± 0.5 (214)			4.4 ± 0.5 (165)					
Body length (cm)												
Male pups	61.7 ± 4.0 (114)			64.1 ± 3.6 (53)			64.5 ± 2.6 (24)					
Female pups	59.2 ± 4.0 (118)			60.4 ± 2.9 (64)			61.9 ± 2.5 (29)					
Body condition												
Male pups	-0.017 ± 0.465 (114)			-0.012 ± 0.479 (53)			-0.116 ± 0.4 (24)					
Female pups	0.026 ± 0.488 (118)			0.087 ± 0.412 (64)			-0.155 ± 0.391 (29)					
Factor	Birth date		Birth mass		Birth length		Birth condition					
	df	F	P	df	F	P	df	F	P	P		
Sex	1	0.03	0.86	1	234.1	<0.001	1	14.4	<0.001	1	0.52	0.47
Year	2	1.10	0.33	2	15.8	<0.001	1	50.3	<0.001	1	1.58	0.21
Year × sex	2	0.81	0.45	2	0.6	0.55	1	3.8	0.05	1	0.22	0.64

Note: Values are given as the mean ± SD, with sample sizes in parentheses. Comparisons between groups (two-way ANOVA) are given considering the 3 years for birth date and body mass at birth, and 1995 and 1996 for body length and body condition at birth.

^aGood/poor class.

^bMales/females.

was not possible. At birth, newborns were caught by hand and individually marked (numbered Velcro glued onto the head) after mother-pup recognition occurred (Roux 1986). They were sexed and weighed (± 0.05 kg) using a spring scale and a rope. In 1995 and 1996, standard body length at birth (from nose to tail (± 1 cm), hereinafter referred to as pup body length) was monitored throughout the pupping period (232 and 117 pups, respectively) using a wooden plank scaled every 1 cm. In 1997, body length of 53 pups was measured at the beginning of the pupping season only. Pup body condition at birth was calculated using the residual values of the linear regression between pup body mass and pup body length at birth (Trites 1992). Because pup body length varies throughout the pupping period, annual comparisons of pup body length and pup body condition at birth were performed without considering 1997.

Maternal body condition

Mothers were not captured at parturition in order to avoid colony disturbance during parturition and bias in the sampling. During the monitoring of parturitions in 1996 and 1997, a score was assigned to each mother based on a visually evaluated index of body condition described in Georges and Guinet (2000b). This allowed us to distinguish mothers in poor condition from those in good condition at parturition (Georges and Guinet 2000b). In 1996, mothers were captured using a collar, restrained on a wooden plank as described by Gentry and Holt (1982), and measured (standard body length ± 1 cm). Mating occurs a few days after parturition, and we used maternal characteristics at parturition as an index of maternal characteristics at mating.

Pup quality over 2 consecutive years

Body mass of pups differed between the sexes and among years. For each pup and each year, we derived an index of pup quality by calculating the deviation m_1 from the mean birth mass according to the equation $m_1 = m - \mu$, where m is the birth mass of the considered pup and μ is the mean birth mass of pups of the same sex born

the same year as the considered pup. For 34 mothers that were known to have reproduced successfully during 2 consecutive years, we investigated the effects of pup characteristics on reproduction in the subsequent season.

Statistical analyses used standard tests (Sokal and Rolf 1981) and were performed using SAS statistical software (SAS Institute Inc., Cary, NC 27513, U.S.A.). Values are given as means ± SD. All tests were two-tailed and differences were considered significant at $P < 0.05$. The experiments complied with current French laws.

Results

Timing of parturition

Births occurred between 20 November and 8 January in all 3 years. Median parturition dates were 12 December in 1995 ($n = 232$) and 1996 ($n = 438$) and 14 December in 1997 ($n = 311$). There were no differences in mean parturition dates among years or between the sexes of pups (two-way ANOVA, $F_{[5,975]} = 0.77$, $P = 0.570$; Table 1).

Maternal characteristics

In 1996 there was a weak but significant relationship between date of parturition (DP, days since 1 November) and maternal body length (MBL, cm) (linear regression, $DP = 7.3 + 0.262MBL$; $r = 0.226$, $n = 91$, $P = 0.032$). Maternal body length was not measured in 1995 and 1997. The numbers of mothers in good versus poor condition did not differ between 1996 and 1997 (χ^2 test, $\chi^2_1 = 2.648$, $P = 0.104$; Table 1). The number of mothers in poor condition did not differ significantly from that of mothers in good condition (1996: $\chi^2_1 = 3.478$, $P = 0.627$; 1997: $\chi^2_1 = 1.183$, $P = 0.881$) and did not vary throughout the parturition period (logistic regression, 1996: $\chi^2_1 = 0.107$, $P = 0.744$; 1997: $\chi^2_1 = 0.019$, $P = 0.89$).

Table 2. ANCOVA of body mass at birth in relation to sex, body length of the pup at birth, year, and their interactions as factors influencing subantarctic fur seals on Amsterdam Island during the 1995 and 1996 pupping seasons.

Factor	df	F	P
Sex	1	151.1	<0.001
Body length	1	155.9	<0.001
Year	1	0.42	0.52
Body length × sex	1	0.48	0.49
Body length × year	1	2.34	0.13
Year × sex	1	1.46	0.23
Year × sex × length	1	0.10	0.75
Error	341		

Pup characteristics at birth

The sex ratio at birth did not differ from unity in any year (1995: $\chi^2_1 = 0.009$, $P = 0.926$; 1996: $\chi^2_1 = 0.018$, $P = 0.892$; 1997: $\chi^2_1 = 1.756$, $P = 0.185$; Table 1). A logistic regression including year and birth date as factors indicates that the sex ratio at birth did not vary between years or across the pupping period ($\chi^2_2 = 3.021$, $P = 0.388$).

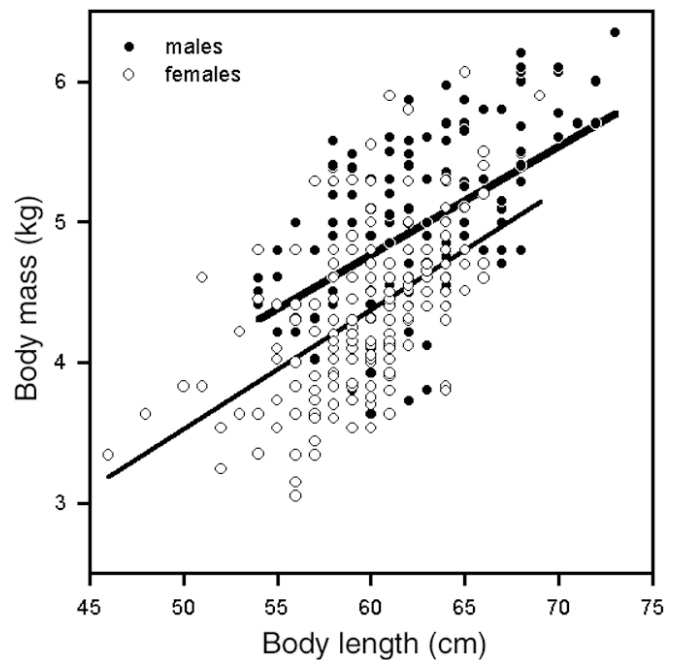
Birth mass and birth length differed between the sexes and among years (two-way ANOVA, birth mass in 1995, 1996, and 1997: $F_{[5,956]} = 53.37$, $P < 0.001$; birth length in 1995 and 1996: $F_{[3,345]} = 22.85$, $P < 0.001$; Table 1), male pups being significantly heavier and longer than female pups at birth every year. Pups of both sexes born in 1996 were heavier and longer than those born in 1995, and male pups born in 1996 were heavier than those born in 1997, whereas female pups born in 1996 were of similar mass to those born in 1997. There were no significant differences in the body condition of male and female pups between 1995 and 1996 ($F_{[3,345]} = 0.77$, $P = 0.511$; Table 1). Interestingly, pup body mass was related to pup sex and body length, but year and interactions had no significant effect (analysis of covariance (ANCOVA) in 1995 and 1996, $F_{[7,341]} = 44.54$, $P < 0.001$; Table 2), indicating that for a given body length, male pups were significantly heavier than female pups (Fig. 1), and that pups born in 1996 were heavier than those born in 1995 because they were longer.

Body mass and length of pups at birth were also related to birth date (three-way ANOVA, body mass in 1995, 1996, and 1997: $F_{[11,950]} = 32.16$, $P < 0.001$; body length in 1995 and 1996: $F_{[7,341]} = 30.48$, $P < 0.001$; Table 3), increasing with birth date (Fig. 2). Body condition of male and female pups at birth was not related to birth date except for female pups in 1996 ($r = 0.30$, $n = 64$, $P = 0.016$; Fig. 2).

Pup characteristics at birth in relation to maternal characteristics

There were no significant differences in maternal body length and maternal body condition between mothers giving birth to male pups and those giving birth to female pups in any year for which data were available (maternal body length in 1996: $t_{[41,481]} = 0.935$, $P = 0.352$; maternal body condition in 1996: $\chi^2_1 = 0.116$, $P = 0.733$; maternal body condition in 1997: $\chi^2_1 = 0.659$, $P = 0.417$). Furthermore, the sex of pups born in 1997 was not related to maternal body length or

Fig. 1. Relationships between body mass and body length at birth in male (thick line) and female (thin line) subantarctic fur seal (*Arctocephalus tropicalis*) pups on Amsterdam Island during the 1995 and 1996 pupping seasons.



maternal body condition the previous year, when mating occurred (logistic regressions, $\chi^2_1 = 0.015$, $P = 0.902$, and $\chi^2_1 = 0.223$, $P = 0.637$, respectively).

In 1996, when maternal body length was measured, pup birth mass was related to the sex of the pup (ANCOVA, $F_{[1,84]} = 20.91$, $P < 0.001$) and increased with maternal body length ($F_{[1,84]} = 25.91$, $P < 0.001$), and there were no differences between the slopes ($F_{[2,84]} = 0.10$, $P = 0.75$; Fig. 3). Pup body mass and body condition at birth were related to maternal body condition for male pups but not for female pups (Tables 4 and 5).

Reproduction over 2 consecutive years

For the 34 mothers that were known to have reproduced successfully in 1996 and 1997, the sex of the pup was not related to maternal body length or to the sex of the pup born the previous year (logistic regression, $\chi^2_2 = 1.382$, $P = 0.501$). The quality (in terms of birth mass; see Methods) of the pup born in 1997 tended to be positively related to the quality of that born in 1996 but was not related to maternal body length or the interaction (Table 6), indicating that, regardless of their body length, mothers gave birth to pups of similar quality. Finally, maternal body condition in 1997 was not related to maternal body condition in 1996 or the sex of the foetus carried (logistic regression, $\chi^2_2 = 3.306$, $P = 0.192$).

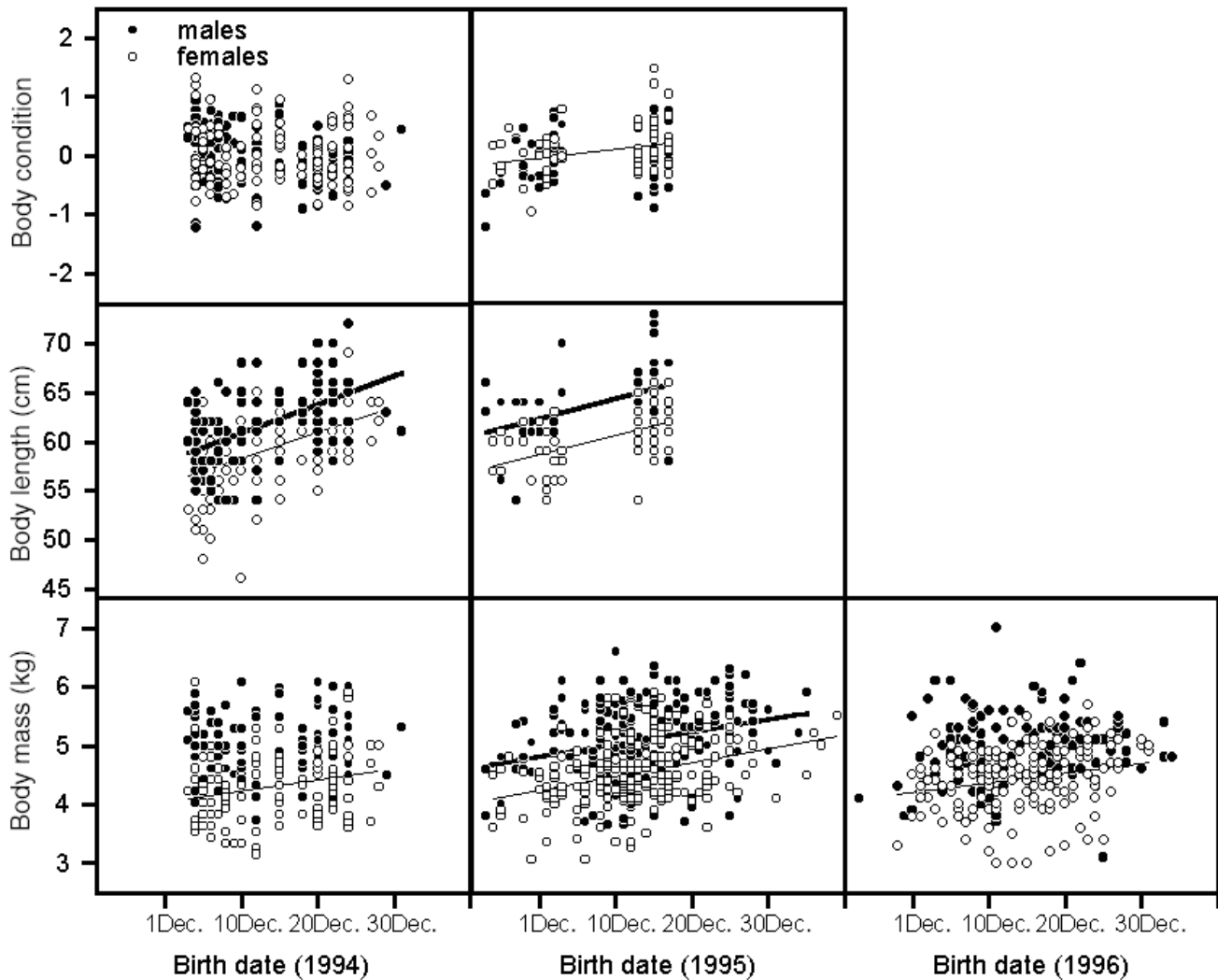
Discussion

In subantarctic fur seals breeding on Amsterdam Island, the sex ratio at birth did not differ from unity and did not vary throughout the pupping period or among years. Furthermore, the sex of the pup was not related to maternal characteristics (body length, body condition) at parturition or when mating occurred 1 year before. This is consistent with

Table 3. ANCOVA of pup body mass, body length, and body condition at birth as dependent variables in relation to the sex of the pup, birth date, year, and their interactions as factors influencing subantarctic fur seals on Amsterdam Island during the 1995, 1996, and 1997 pupping seasons.

Factor	Body mass (1995, 1996, and 1997)			Body length (1995 and 1996)			Body condition (1995 and 1996)		
	df	F	P	df	F	P	df	F	P
Sex	1	249.53	<0.001	1	67.33	<0.001	1	1.62	0.20
Birth date	1	62.26	<0.001	1	83.02	<0.001	1	0.00	0.95
Year	2	16.89	<0.001	1	58.01	<0.001	1	0.53	0.47
Birth date × sex	1	1.83	0.18	1	0.00	0.95	1	0.71	0.40
Birth date × year	2	2.29	0.11	1	2.89	0.09	1	11.76	<0.001
Year × sex	2	0.64	0.53	1	1.91	0.17	1	0.47	0.49
Year × sex × birth date	2	0.30	0.74	1	0.05	0.82	1	0.50	0.48
Error	950			341			341		

Fig. 2. Relationships between body mass, body length, and body condition at birth and birth date in male (thick line) and female (thin line) subantarctic fur seal pups on Amsterdam Island during the 1995, 1996, and 1997 pupping seasons. Birth dates were recorded as days after 1 November.



Clutton-Brock's (1991) conclusion that cases where the sex ratio at birth differs from the foetal sex ratio are rare in mammals. Previous studies in ungulates have shown that the offspring sex ratio is affected by maternal age or condition (Verme 1983; Skogland 1986; Clutton-Brock 1991),

whereas Hewison and Gaillard (1999) pointed out that this is not always the case. The theoretical model of Trivers and Willard (1973) predicts that in polygynous species, natural selection will favour maternal ability to adjust the sex ratio of offspring produced and (or) to bias investment toward the

Fig. 3. Relationship between body mass of subantarctic fur seal pups at birth and maternal body length for male (thick line) and female (thin line) pups on Amsterdam Island during the 1996 pupping season.

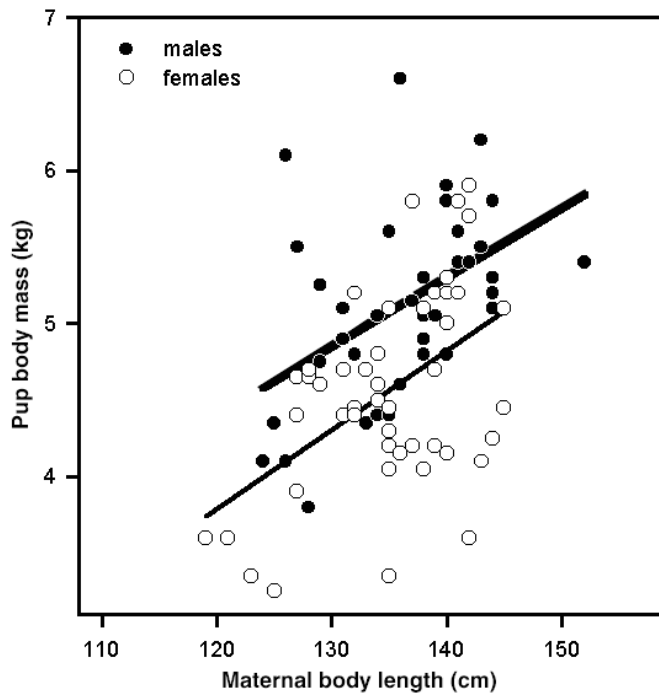


Table 4. Pup body mass at birth according to the sex of the pup and maternal body condition in subantarctic fur seal pups on Amsterdam Island during the 1996 and 1997 pupping seasons.

	Maternal body condition		
	Poor	Good	
Pup body mass at birth			
1996			
Males	5.0 ± 0.6 (71)	5.3 ± 0.5 (57)	
Females	4.6 ± 0.5 (77)	4.6 ± 0.5 (56)	
1997			
Males	4.8 ± 0.5 (55)	5.2 ± 0.6 (34)	
Females	4.5 ± 0.4 (78)	4.4 ± 0.5 (39)	
Factor	df	F	P
Sex	1	117.87	<0.001
MBC	1	20.95	<0.001
Year	2	19.06	<0.001
MBC × sex	1	6.12	0.01
MBC × year	2	1.05	0.31
Year × sex	2	0.44	0.51
Year × sex × MBC	2	0.08	0.78
Error	458		

Note: Values are given as the mean ± SD, with sample sizes in parentheses. The results of the ANCOVA of pup body mass at birth in relation to sex, maternal body condition (MBC), year, and their interactions as factors are also given.

more profitable sex, according to her ability to invest. In fur seals, high-quality mothers (in terms of body size) rear high-quality offspring (Calambokidis and Gentry 1985; Boltnev et al. 1998; Georges and Guinet 2000a), and it is likely that

Table 5. Body condition of the pup according to maternal body condition at parturition in subantarctic fur seal pups on Amsterdam Island during the 1996 pupping season.

	Good condition	Poor condition	U	P
Male pups	0.243 ± 0.442 (17)	-0.059 ± 0.428 (20)	103	0.041
Female pups	0.114 ± 0.447 (17)	0.179 ± 0.420 (28)	285	0.266

Note: Values are given as the mean ± SD, with sample sizes in parentheses.

Table 6. Effect of pup quality in the first year and maternal body length (MBL) on pup quality in the second year for subantarctic fur seal mothers that reproduced successfully on Amsterdam Island during the 1996 and 1997 pupping seasons.

Factor	df	F	P
Pup quality, 1996	1	2.89	0.09
MBL	1	0.31	0.58
MBL × pup quality	2	1.7	0.20
Error	30		

differences in quality between offspring at weaning persist to adulthood, as is found in phocid seals (Fedak and Anderson 1982). Accordingly, fur seal mothers in good condition are expected to produce a higher proportion of male than female pups compared with mothers in poor condition. However, our data on sex ratio and body condition at birth do not fit this model, as is also observed for other otariids such as the Galapagos (*Arctocephalus galapagoensis*; Trillmich 1986), Antarctic (Boyde and McCann 1989; Lunn and Arnould 1997), northern (*Callorhinus ursinus*; Trites 1991), and Cape (*Arctocephalus pusillus pusillus*; Mison-Jooste 1999) fur seals, and California sea lion (*Zalophus californianus*; Ono and Boness 1996). These results suggest that the polygyny and sexual dimorphism observed in pinnipeds do not induce a sex-ratio adjustment.

Male subantarctic fur seal pups were significantly heavier than female pups at birth for all years, as is widely observed in pinnipeds (southern elephant seals (*Mirounga leonina*), Anderson and Fedak 1985; McCann et al. 1989; grey seals (*Halichoerus grypsus*), Kovacs and Lavigne 1986; harbour seals (*Phoca vitulina*), Bowen et al. 1994; Galapagos fur seals, Trillmich 1986; Antarctic fur seals, Doidge et al. 1986; northern fur seals, Trites 1993; Cape fur seals, Mison-Jooste 1999). Male pups were also longer than female pups at birth, which suggests that male foetuses grew faster than female foetuses, as is suggested for northern fur seals (Trites 1991). Pup body mass and body length at birth were positively related to birth date in most cases, but pup body condition did not vary throughout the pupping season, suggesting that in most cases, pups born later in the season tended to be heavier because they were longer and not because they were in better condition. Interestingly, in 1996, the increase in body length and consequently in body mass was associated with an increase in body condition in female pups but not in male pups. This suggests two different growth strategies, with male pups growing in length (i.e., skeletal growth), whereas females appear to grow in body mass (tissue growth). In our study, the increase in birth body mass throughout the pupping season

Table 7. Estimated total body gross energy (TBGE) at birth in subantarctic fur seal pups on Amsterdam Island during the 1995, 1996, and 1997 pupping seasons.

Year	Total body gross energy (MJ)		<i>t</i>	<i>P</i>
	Male pups	Female pups		
1995	23.2 ± 7.6 (114)	20.8 ± 8.7 (118)	2.178	0.03
1996	26.0 ± 8.6 (220)	24.6 ± 8.0 (214)	1.82	0.064
1997	23.8 ± 7.8 (130)	22.9 ± 8.0 (165)	0.976	0.33

Factor	df	<i>F</i>	<i>P</i>
Year	2	13.3	<0.001
Sex	1	8.2	0.004
Year × sex	2	0.5	ns

Note: Values are given as the mean ± SD, with sample sizes in parentheses; ns, not significant. Means are compared among groups for each variable according to two-way ANOVA. TBGE was estimated assuming that the formulae obtained for Antarctic fur seals hold for subantarctic fur seals: males: total body water (TBW) = 1.31 + 0.51 × body mass; females: TBW = 1.26 + 0.48 × body mass; both sexes: TBGE = 31.7 – 0.347 × TBW; masses are given in kilograms and TBW as a percentage (from Arnould et al. 1996a, 1996b).

was associated with an increase in maternal body length, while there were no trends in maternal body condition, suggesting that independently of their body condition, longer mothers gave birth to heavier pups and tended to do so later in the season. In fur seals, body length increases throughout life (Trites and Bigg 1996), and longer individuals are expected to be older, and thus more experienced (Lunn et al. 1994). Similarly, older/longer Cape fur seals give birth later in the season (Rand 1955), while pup body mass at birth increases throughout the pupping period (Mison-Jooste 1999). Inversely, in Antarctic fur seals pup body mass at birth decreases throughout the pupping period and this is associated with a decrease in maternal body length (Boyd and McCann 1989; Lunn and Boyd 1993a). These covariances are consistent with the positive relationship found between maternal body length and pup body mass at birth in both species (Boyd and McCann 1989; this study) and also in harbour seals (Bowen et al. 1994). Differences in the timing of parturition related to maternal age seem to result from differences in life-history traits between Cape/subantarctic fur seals (10 months of lactation) and Antarctic fur seals (4 months of lactation; see also Georges and Guinet 2000b).

Mothers in good condition at parturition gave birth to heavier sons (which were also in better condition) than mothers in poor condition, whereas no similar relationship was found for daughters. In other words, mothers appear to produce sons that are as large as possible, whereas they produce daughters that are equal in quality based on their physiological state. Costa et al. (1988) found that during years of low food availability, Antarctic fur seals give birth to sons of similar sizes whatever their body condition, while mothers in poor condition give birth to lighter daughters than mothers in good condition. Boyd and McCann (1989) found a relationship similar to ours between maternal condition and birth mass in Antarctic fur seal pups according to sex during years of normal food availability, but Lunn and Boyd (1993a) also found the same relationship as ours during years of low food availability. It is interesting to point out that what we found for sons is consistent with state-dependent life-history theory, which predicts that the quality of offspring will depend on the state of the mother (McNamara and Houston 1996). The fact that we did not find the same pattern for daughters suggests that male and female foetuses may

extract maternal resources differently during gestation: our results show that for a given body length, male subantarctic fur seal pups were heavier than females at birth (Fig. 1), indicating that male pups were denser than female pups at birth. In view of the difference in density between lean and fat tissues, these results also suggest that for a given body mass at birth, daughters should have more fat than sons. Such suggested sex-related differences in body composition may explain the differences in the way maternal resources are used by male and female foetuses during gestation. Sex-related differences in body composition have also been reported in Antarctic fur seals, where male pups are heavier and leaner than female pups, resulting in similar levels of total body gross energy between the sexes (Arnould et al. 1996a). Interestingly, these authors established the relationship between total body water and body mass for each sex in Antarctic fur seal pups (Arnould et al. 1996a), while Arnould et al. (1996b) proposed a relationship between total body water and total body gross energy (TBGE). Using the mean values derived from these formulae (see Table 7), and assuming that these relationships hold for subantarctic fur seals, one may estimate TBGE in subantarctic fur seal pups according to their body mass at birth (Table 7). These estimates suggest that TBGE at birth would tend to be higher in males than in females for 2 of the 3 years. Since measurements of body composition are needed to assess the actual amount of energy in male and female foetuses in subantarctic fur seals, these estimates suggest that the costs of carrying a male foetus are higher than those of carrying a female foetus. Consistently, the sex-related relationships we found between maternal body condition and pup body mass/condition at birth indicate that mothers carrying a male foetus appear to enhance foetal growth only when their body condition allows them to do so. Moreover, recent results obtained from Cape fur seals show that during years of low food availability, i.e., when maternal body condition is low, the abortion rate is higher in mothers carrying male foetuses than in those carrying female foetuses (Mison-Jooste 1999), which supports our hypothesis that for fur seals, the costs of carrying a male foetus are higher than those of carrying a female foetus.

Pups were heavier at birth in 1996 than in 1995 and 1997. They were also longer in 1996 than in 1995, while body condition at birth did not differ significantly among years, indi-

cating that pups were heavier in 1996 because they were longer and not because they were in better condition. Previous studies had shown that foetal growth rate and pup birth mass were related to environmental conditions or to the growth of the pup born in the previous year used as an index of prey availability during gestation (Trillmich and Limberger 1985; Trites 1992; Lunn and Boyd 1993*b*; Mison-Jooste 1999). In the present study, annual variation in pup body mass at birth suggests that prey availability was relatively low, intermediate, and high during the gestation of pups born in 1995, 1997, and 1996, respectively. This is supported by previous results indicating that mortality calculated during the first weeks of life was lower in pups born in 1996 than in 1997 (Georges and Guinet 2000*b*).

In the present study, mothers gave birth to pups that were similar in quality (considering the variation in pup body mass at birth between the sexes and among years) from one year to the next, regardless of their body length. This suggests that independent of their age, mothers are of consistent quality among years, though some individuals have a higher reproductive value (in terms of pup mass at birth) than others. Interestingly, the sex of the pup was not related to the sex of the previous one, and maternal body condition at parturition was not related to the sex of the foetus carried. In ungulates, the higher cost of sons has been shown to be associated with a lower probability of producing male offspring in consecutive years (Festa-Bianchet 1989; Bérubé et al. 1996). Our results suggest that in subantarctic fur seals, future reproduction does not seem to be affected by the apparently higher costs of carrying male foetuses, probably because foetal growth constitutes a minor part of the maternal energy budget for reproduction, as was proposed for Antarctic fur seals (Boyd and McCann 1989). However, in subantarctic fur seals, in which lactation seems to compete with gestation during the austral winter (Georges and Guinet 2000*a*), prey availability should be an important factor in foetal growth. This would be particularly true during the last months that pregnant mothers spend at sea, as about 50% of the growth occurs in the final month of gestation (Frazer and Huggett 1974). Thus, maternal characteristics and environmental conditions appear to act on birth size, which in turn is known to determine growth and survival in fur seals (Calambokidis and Gentry 1985; Boltnev et al. 1998; Georges and Guinet 2000*a*, 2000*b*).

In short, our results and estimates suggest that (i) more energy appears to be allocated during gestation by mothers carrying male foetuses than by those carrying female foetuses, but there is little evidence for differential reproductive costs of producing male or female foetuses, (ii) the way in which resources are used by the foetus depends on its sex, resulting in two different growth strategies related to sex differences in body composition, and (iii) a mother's reproductive value is independent of her age, but environmental (trophic) conditions and consequent maternal body condition during gestation are important components of maternal investment.

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References

- Alexander, R.D., Hoogland, J.L., Howard, R.D., Noonan, K.M., and Sherman, P.W. 1979. Sexual dimorphisms and breeding systems in pinnipeds, ungulates, primates and humans. *In* Evolutionary biology and human sexual behavior: an anthropological perspectives. *Edited* by N.A. Chagnon and W. Irons. Duxbury, Mass. pp. 402–435.
- Anderson, S.S., and Fedak, M.A. 1985. Grey seal males: energetic and behavioural links between size and sexual success. *Anim. Behav.* **33**: 829–838.
- Arnould, J.P.Y., Boyd, I.L., and Socha, D.G. 1996*a*. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. *Can. J. Zool.* **74**: 254–266.
- Arnould, J.P.Y., Boyd, I.L., and Speakman, J.R. 1996*b*. Measuring the body composition of Antarctic fur seals (*Arctocephalus gazella*): validation of hydrogen isotope dilution. *Physiol. Zool.* **69**: 93–116.
- Bérubé, C.H., Festa-Bianchet, M., and Jorgenson, J.T. 1996. Reproductive costs of sons and daughters in Rocky Mountain bighorn sheep. *Behav. Ecol.* **7**: 60–68.
- Boltnev, A.I., York, A.E., and Antonelis, G.A. 1998. Northern fur seal young: interrelationships among birth size, growth, and survival. *Can. J. Zool.* **76**: 843–854.
- Bowen, W.D., Oftedal, O.T., Boness, D.J., and Iverson, S.J. 1994. The effect of maternal age and other factors on birth mass in the harbour seal. *Can. J. Zool.* **72**: 8–14.
- Boyd, I.L., and McCann, T.S. 1989. Pre-natal investment in reproduction by female Antarctic fur seals. *Behav. Ecol. Sociobiol.* **24**: 377–385.
- Calambokidis, J., and Gentry, R.L. 1985. Mortality of northern fur seal pups in relation to growth and birth weights. *J. Wildl. Dis.* **21**: 327–330.
- Carranza, J. 1996. Sexual selection for male body mass and the evolution of litter size in mammals. *Am. Nat.* **148**: 81–100.
- Charnov, E.L. 1982. The theory of sex allocation. Princeton University Press, Princeton, N.J.
- Clutton-Brock, T.H. 1988. Reproductive success. *In* Reproductive success: studies of individual variation in contrasting breeding systems. *Edited* by T.H. Clutton-Brock. University of Chicago Press, Chicago. pp. 472–485.
- Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton University Press, Princeton, N.J.
- Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1982. Red deer: the behaviour and ecology of two sexes. University of Chicago, Chicago.
- Costa, D.P., Trillmich, F., and Croxall, J.P. 1988. Intraspecific allometry of neonatal size in the Antarctic fur seal (*Arctocephalus gazella*). *Behav. Ecol. Sociobiol.* **22**: 361–364.
- Doidge, D.W., McCann, T.S., and Croxall, J.P. 1986. Attendance behavior of Antarctic fur seals. *In* Fur seals: maternal strategies on land and at sea. *Edited* by R.L. Gentry and G.L. Kooyman. Princeton University Press, Princeton, N.J. pp. 102–114.
- Duck, C.D. 1990. Annual variation in the timing of reproduction in

- Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South Georgia. *J. Zool. (Lond.)*, **222**: 103–116.
- Fedak, M.A., and Anderson, S.S. 1982. The energetics of lactation: accurate measurements from a large wild mammal, the grey seal (*Halichoerus grypus*). *J. Zool. (1964–1985)*, **198**: 473–479.
- Festa-Bianchet, M. 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes. *J. Anim. Ecol.* **58**: 785–795.
- Fisher, R.A. 1930. The genetical theory of natural selection. Oxford University Press, Oxford.
- Frank, S.A. 1990. Sex allocation theory for birds and mammals. *Annu. Rev. Ecol. Syst.* **21**: 13–55.
- Frazer, J.F.D., and Huggett, A.S.G. 1974. Species variations in the foetal growth rates of eutherian mammals. *J. Zool. (1964–1985)*, **174**: 481–509.
- Gentry, R.L., and Holt, J.R. 1982. Equipment and techniques for handling northern fur seals. NOAA Tech Rep. NMFS SSRF 758.
- Georges, J.Y., and Guinet, C. 2000a. Maternal care in the subantarctic fur seals on Amsterdam Island. *Ecology*, **81**: 295–308.
- Georges, J.Y., and Guinet, C. 2000b. Early mortality and perinatal growth in the subantarctic fur seals *Arctocephalus tropicalis* on Amsterdam Island. *J. Zool. (Lond.)*, **251**: 277–287.
- Goldsworthy, S.D., and Saughnessy, P.D. 1994. Breeding biology and haul-out pattern of the New Zealand fur seal, *Arctocephalus forsteri*, at Cape Gantheaume, South Australia. *Wild. Res.* **21**: 365–376.
- Guinet, C., Jouventin, P., and Georges, J.Y. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St. Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. *Antarct. Sci.* **6**: 473–478.
- Hewison, A.J.M., and Gaillard, J.M. 1999. Successful sons or advantaged daughters? The Trivers–Willard model and sex-biased maternal investment in ungulates. *Trends Ecol. Evol.* **14**: 229–234.
- King, J.E. 1983. Seals of the world. Oxford University Press, Oxford.
- Kovacs, K.M., and Lavigne, D.M. 1986. Growth of grey seal (*Halichoerus grypus*) neonates: differential maternal investment in the sexes. *Can. J. Zool.* **64**: 1937–1943.
- Le Boeuf, B.J., and Reiter, J. 1988. Lifetime reproductive success in northern elephant seals. In *Reproductive success*. Edited by T.H. Clutton-Brock. University of Chicago, Chicago. pp. 344–362.
- Lunn, N.J., and Arnould, J.P.Y. 1997. Maternal investment in Antarctic fur seals: evidence for equality in the sexes? *Behav. Ecol. Sociobiol.* **40**: 351–362.
- Lunn, N.J., and Boyd, I.L. 1993a. Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *J. Zool. (Lond.)*, **229**: 55–67.
- Lunn, N.J., and Boyd, I.L. 1993b. Influence of maternal characteristics and environmental variations on reproduction in Antarctic fur seals. *Symp. Zool. Soc. Lond. No. 66*. pp. 115–129.
- Lunn, N.J., Boyd, I.L., and Croxall, J.P. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. *J. Anim. Ecol.* **63**: 827–840.
- Maynard Smith, J. 1980. A new theory of sexual investment. *Behav. Ecol. Sociobiol.* **7**: 247–251.
- McCann, T.S. 1980. Territoriality and breeding behaviour of adult male Antarctic fur seals, *Arctocephalus gazella*. *J. Zool. (1964–1985)*, **192**: 295–310.
- McCann, T.S., Fedak, M.A., and Harwood, J. 1989. Parental investment in southern elephant seals, *Mirounga leonina*. *Behav. Ecol. Sociobiol.* **25**: 81–87.
- McNamara, J.M., and Houston, A.I. 1996. State-dependent life histories. *Nature (Lond.)*, **380**: 215–221.
- Mison-Jooste, V. 1999. Contribution à l'étude de la biologie des populations de l'otarie à fourrure du Cap (*Arctocephalus pusillus pusillus*): les soins maternels différent-ils en fonction du sexe du jeune? Ph.D. thesis, University Claude-Bernard, Lyon, France.
- Ono, K.A., and Boness, D.J. 1996. Sexual dimorphism in sea lion pups: differential maternal investment, or sex-specific differences in energy allocation? *Behav. Ecol. Sociobiol.* **38**: 31–41.
- Ono, K.A., Bonness, D.J., and Oftedal, O.T. 1987. The effect of a natural environment disturbance on maternal investment and pup behavior in the Californian sea lion. *Behav. Ecol. Sociobiol.* **21**: 109–118.
- Rand, R.W. 1955. Reproduction in Cape fur seal, *Arctocephalus pusillus pusillus*. *Proc. Zool. Soc. Lond.* **124**: 717–740.
- Roux, J.P. 1986. Sociobiologie de l'otarie *Arctocephalus tropicalis*. Ph.D. thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France.
- Skogland, T. 1986. Sex ratio variation in relation to maternal condition and parental investment in wild reindeer *Rangifer t. tarandus*. *Oikos*, **46**: 417–419.
- Sokal, R.R., and Rolf, F.J. 1981. Biometry. W.H. Freeman and Sons, New York.
- Stamps, J.A. 1990. When should avian parents differentially provision sons and daughters? *Am. Nat.* **135**: 671–685.
- Trillmich, F. 1986. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. *Behav. Ecol. Sociobiol.* **19**: 157–164.
- Trillmich, F. 1996. Parental investment in pinnipeds. *Adv. Study Behav.* **25**: 533–577.
- Trillmich, F., and Limberger, D. 1985. Drastic effects of El Niño on Galapagos pinnipeds. *Oecologia*, **67**: 19–22.
- Trites, A.W. 1991. Foetal growth of northern fur seals: life-history strategy and sources of variation. *Can. J. Zool.* **69**: 2608–2617.
- Trites, A.W. 1992. Foetal growth and the condition of pregnant northern fur seals off western North America from 1958 to 1972. *Can. J. Zool.* **70**: 2125–2131.
- Trites, A.W. 1993. Biased estimates of fur seal pup mass: origins and implications. *J. Zool. (Lond.)*, **229**: 515–525.
- Trites, A.W., and Bigg, M.A. 1996. Physical growth of northern fur seals (*Callorhinus ursinus*): seasonal fluctuations and migratory influences. *J. Zool. (Lond.)*, **238**: 459–482.
- Trivers, R.L. 1972. Parental investment and natural selection. In *Sexual selection and the descent of man*. Edited by B. Campbell. Aldine, Chicago. pp. 136–149.
- Trivers, R.L., and Willard, D.E. 1973. Natural selection of parental ability to vary the sex ratio of offspring. *Science (Washington, D.C.)*, **179**: 90–92.
- Verme, L.J. 1983. Sex ratio variation in *Odocoileus*: a critical review. *J. Wildl. Manag.* **47**: 573–582.